THE HETEROECISM OF PUCCINIA MONTANENSIS, P. KOELERIAE, AND P. APOCRYPTA[1]

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(WITH TEXT FIGURES 1–4)

Puccinia montanensis Ellis, *P. Koeleriae* Arth., and *P. apocrypta* Ellis & Tracy belong to the group of grass rusts having long-covered telia to which *P. triticina* Erikss. and *P. secalina* Grove (*P. dispersa* Erikss.) belong. In connection with the investigation of the last-named rusts, which is being conducted by this laboratory in coöperation with the Office of Cereal Investigations of the U. S. Department of Agriculture, some attention has been given to a study of the related rusts of this group as a part of the general rust investigations of the laboratory, for the help which such a study will afford in the solution of cereal rust problems. In connection with this work considerable taxonomic study of the material in the Arthur herbarium has been necessary, which has resulted in a partial realignment of the rusts involved and has formed the basis for the treatment of these as finally published in the North American Flora.[2]

PUCCINIA MONTANENSIS

Of the three rusts *Puccinia montanensis* is perhaps the most distinctive. It was described by Ellis[3] from a collection upon *Elymus*

[1] Contribution from the Botanical Department of the Purdue University Agricultural Experiment Station. This work is in part a result of the studies being conducted cooperatively between that Department and the Office of Cereal Investigation, Bureau of Plant Industry, U. S. Department of Agriculture.

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[2] Arthur, J. C., & Fromme, F. D. Dicaeoma on Poaceae. North American Flora **7**: 325, 330 and 332. 1920.

[3] Ellis, J. B. Descriptions of Some New Species of Fungi. Journ. Mycol. **1**: 274. 1893.

condensatus made by Rev. F. D. Kelsey at Helena, Montana, July, 1891. An examination of the type (Ellis & Ev., N. Am. Fungi 2892) shows that this rust is to be distinguished from the other grass rusts having long-covered telia by the arrangement of the uredinia and telia in lines, by the broad teliospores and the abundant thin-walled paraphyses bordering the uredinia (fig. 1). In

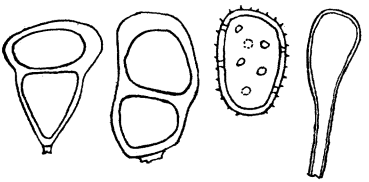

FIG. 1. Teliospores, urediniospore and uredinial paraphysis from the type specimen of *P. montanensis* (x 400).

1915 Arthur[4] sowed aeciospores from *Hydrophyllum capitatum,* obtaining uredinia and telia upon *Agropyron tenerum* and uredinia upon *Elymus virginicus.* This material was determined as *Puccinia montanensis,* and on this basis the Hydrophyllaceous and Boraginaceous aecia of the United States have been considered as belonging to this species.

AECIAL RELATIONSHIP OF PUCCINIA MONTANENSIS

In the spring of 1919 two collections of *Puccinia montanensis,* one upon *Elymus canadensis* and the other upon *Agropyron* sp., made by H. S. Jackson at Boulder, Colo., Nov. 12, 1918, were found to be viable. On the assumption that they should produce aecia upon Boraginaceous or Hydrophyllaceous species, these collections were sown on *Myosotis palustris, Phacelia Purshii, Nyctelea Nyctelea,* and *Hydrophyllum* sp. without obtaining infection. Later in the same summer Mr. E. Bethel sent collections of a rust on *Agropyron tenerum, Agropyron Smithii* and *Hordeum jubatum* which he had collected with Dr. G. H. Coons at Mancos, Colo. Accompanying this material was a collection of aecia on *Berberis Fendleri,* which he stated was so closely associated with the grass rust as to suggest relationship. Such an association did not neces-

[4] Arthur, J. C. Cultures of Uredineae in 1915. Mycologia 8: 137–139. 1915.

sarily mean a connection between the two forms, as the grass rust may have come from aecia upon a plant which had died down and disappeared earlier in the season. Mr. Bethel remarked that the situation was made the more difficult to explain by the absence of *Koeleria cristata,* the grass host supposedly connected with the *Berberis* aecia. On this account, and because of the insistence of Dr. Coons that there must be some connection between the aecia upon *Berberis Fendleri* and the associated grass rust, he sent the material for culture and study. An examination of the material showed that the rust on *Berberis Fendleri* was *Aecidium Fendleri* Tracy & Earle, and that on the grasses was *Puccinia montanensis.* As such a connection would add an entirely new aecial host in a genus rather far removed from *Hydrophyllum,* it became important to establish or disprove this by cultures. The aeciospores, proving viable, were sown and produced infection upon *Hordeum jubatum* and *Hystrix Hystrix.* In the meantime Mr. Bethel made a sowing in his garden at Denver, Colo., from a part of the same collection of aecia and obtained infection upon *Agropyron tenerum.* Mr. Bethel was kind enough to send some of this material to me for study.

Further evidence of this connection was obtained from cultures made in the spring of 1920. Four collections gave infection upon *Berberis Fendleri.* Of these, three were from Mancos, Colo., on *Agropyron tenerum, A. Smithii* and *Agropyron* sp., rusted grasses associated with the *Berberis Fendleri* used in the aecial culture mentioned above. The fourth culture was from telia obtained by Mr. Bethel at Denver by sowing the above aecial material on *Agropyron tenerum.* Ten other collections, eight from Colorado and two from Indiana, were sown on *Berberis Fendleri* without infection. In most of these cases the teliospores germinated weakly, and this may account, in part at least, for the negative results.

A careful comparison was made of the material obtained from the above cultures with the type of *P. montanensis.* It was found that all the material, shown by these cultures to be connected with aecia on *Berberis Fendleri,* agreed closely with the type of *P. montanensis.* The uredinia are cinnamon-brown and are provided

with an abundance of thin-walled, peripheral paraphyses (fig. 2), giving the sori a fringed appearance under the binocular. The

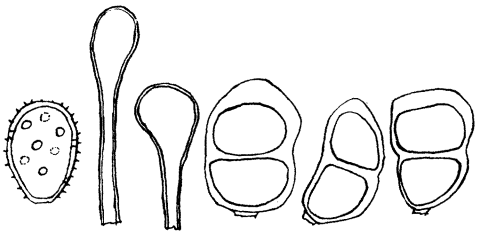

FIG. 2. Urediniospore, uredinial paraphyses and teliospores of *P. montanensis* obtained from culture of *Aecidium Fendleri* on *Hystrix Hystrix* (× 400).

urediniospores are 19–26 by 21–34 μ and have brown walls and 8–10 scattered germ pores. The teliospores are broad, 18–34 by 35–64 μ (fig. 2), and have rather thick walls.

On the other hand, a comparison of the above material with that resulting from the cultures with *Hydrophyllum* aecia mentioned above (Arthur l. c. 4) showed points of marked difference. The uredinia and telia connected with the *Hydrophyllum* aecia are scattered or loosely grouped. The uredinia are yellow and without paraphyses. The urediniospores are 13–21 by 19–25 μ and have pale yellow or colorless walls with 6–8 scattered germ pores. The teliospores are narrow, 13–23 by 32–48 μ, with thin walls except for the apical thickening (fig. 3). On the basis of the above cul-

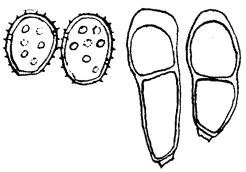

FIG. 3. Urediniospores and teliospores of *P. apocrypta* on *Elymus virginicus* obtained by culture with aeciospores from *Hydrophyllum capitatum* (× 400).

tures, therefore, *Berberis Fendleri* must be considered as the only proven aecial host of this rust. That other aecial hosts exist is a possibility. The geographic distribution of *P. montanensis,* as indicated by specimens in the herbarium, is British Columbia, Wis-

consin, Indiana, southward to New Mexico and southern California, while *Berberis Fendleri* is limited in its distribution to the mountains of Colorado and New Mexico. Such a difference in distribution, however, would be explained if this rust is not dependent upon its aecial stage, but is able to overwinter in the uredinial stage. Mr. Bethel has made observations in Colorado which indicate that such an overwintering may occur there. It is probable, however, that part of the negative results obtained by culturing *P. montanensis* on *Berberis Fendleri* can be explained only by the presence of races in this rust going to different aecial hosts. From present information it is impossible to foretell what these hosts may be. They may be other species of *Berberis* or *Mahonia* or possibly species of some closely allied family. For the present the most that can be said is that *Puccinia montanensis*, in part at least, has *Berberis Fendleri* as its aecial host.

AECIA OF PUCCINIA MONTANENSIS

A study to determine the identity of the aecia on *Berberis Fendleri* obtained from the above-described cultures resulted in finding that they agree with the type of *Aecidium Fendleri* Tracy & Earle. This type also was collected at Mancos, Colo., and Mr. Bethel assures me it was collected at the same place where the material used in the above cultures was obtained. The culture material and the type agree in having aeciospores 18–23 by 20–30 μ. As aecia on *Berberis Fendleri* and the closely related *Mahonia Aquifolium* have been considered as belonging to *Puccinia Koeleriae* Arth., it became necessary to make a study of the latter rust in comparison with *P. montanensis*.

PUCCINIA KOELERIAE

Puccinia Koeleriae Arth.[5] (p. 247) was based on material resulting from cultures in which aecia were produced upon *Mahonia Aquifolium* (Pursh.) Nutt. from teliospores on *Koeleria cristata*. An examination of the type of this species which was collected by E. Bethel at Ouray, Colo., Aug. 23, 1907, shows that it has scat-

[5] Arthur, J. C. Cultures of Uredineae in 1908. Mycologia 1: 225–256. 1909.

tered uredinia and telia, uredinia with thick-walled (1.5–3 μ), peripheral paraphyses (fig. 4), and narrow teliospores, 15–21 by 45–55 μ. In these characters of the uredinia and telia, therefore, *Puccinia Koeleriae* shows a number of important differences from

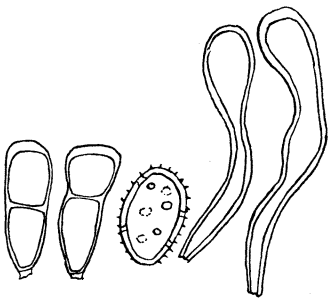

FIG. 4. Teliospores, urediniospore and uredinial paraphyses from the type specimen of *P. Koeleriae* (× 400).

P. montanensis and must be considered as a distinct species, while showing relationship in that both possess abundant paraphyses and urediniospores with brown, thick walls and 8–10 scattered pores.

PUCCINIA APOCRYPTA

A study was made of the rust used by Arthur (l. c. 4) in the cultures of the *Hydrophyllum* aecia mentioned above, in order to establish its identity. As the result of this study it was decided that the rust in question probably was *Puccinia apocrypta* Ellis & Tracy. This rust was described by Ellis & Tracy[6] from material collected by Tracy at Cañon City, Colo., Aug., 1887, on *"Asprella Hystrix,"* which host determination Arthur[7] (p. 138) has shown probably was an error for *Sitanion elymoides*. An examination of this material shows that *Puccinia apocrypta* is very distinct from both *P. montanensis* and *P. Koeleriae,* being distinguished by its smaller, paler urediniospores having fewer germ pores and by the absence of paraphyses in the uredinium. Still further cultural evidence of the aecial relationship of this rust was obtained when, in June,

[6] Ellis, J. B., and Tracy, S. M. A Few New Fungi. Journ. Mycol. **6**: 76–77. 1890.

[7] Arthur, J. C. Cultures of Uredineae in 1915. Mycologia **8**: 125–141. 1916.

1919, Mr. G. R. Hoerner sent a collection of aecia on *Hydrophyllum* obtained at Corvallis, Oregon. Aeciospores from this collection were sown, obtaining infection upon *Elymus virginicus*, with a slight development on *Elymus canadensis* and *Triticum aestivum*, both of the latter, however, proving not to be congenial hosts. A study of the *Elymus virginicus* material showed that it agreed with the other material of *P. apocrypta*.

DISCUSSION

The foregoing work, while by no means settling the complete aecial relationships of these rusts, has resulted in a realignment of them, which, it is felt, is more in keeping with their morphology. *Puccinia montanensis*, so long as it was considered as having its aecia on *Hydrophyllum*, invited comparison with such species as *Puccinia bromina* Erikss. on *Bromus* and *P. secalina* Grove (*P. dispersa*) on rye, both of which have their aecia on the closely allied family, Boraginaceae. From both of these species *P. montanensis* is distinguished, among other characters, by possessing abundant paraphyses in the uredinium, these being practically lacking in both *P. bromina* and *P. secalina*. *Puccinia montanensis* with aecia on *Berberis*, however, invites comparison with other species of rust with long-covered telia having aecia on species of the Berberidaceae. Such species are *Puccinia Koeleriae* in North America with aecia on *Mahonia Aquifolium* and *Puccinia Arrhenatheri* in Europe with aecia on *Berberis vulgaris*. Both the latter rusts agree with *Puccinia montanensis* in possessing abundant paraphyses in the uredinium. In *Puccinia apocrypta*, on the other hand, having *Hydrophyllum* for its aecial host, we have a rust which with its lack of paraphyses, at least, agrees with *P. bromina* and *P. secalina*. It is true that *P. apocrypta* differs from both of the latter in its smaller urediniospores with lighter colored walls, but similar differences can be found in the grass rusts among those having species of Ranunculaceae for their aecial hosts.

It is difficult, of course, to say what other species may serve as aecial hosts for the above rusts besides those shown by culture. It would appear that *Puccinia montanensis* consists of several races, one of which goes to *Berberis Fendleri*. It is not possible at the

present time to say what the aecial hosts of the other race or races may be, but they are likely to be some other species of the Berberidaceae or some closely allied family. *Puccinia apocrypta* presents a somewhat similar situation. As this rust, however, has been cultured only by sowing aeciospores from *Hydrophyllum* on grass hosts, no cultures having been successfully made by sowing teliospores upon a series of Hydrophyllaceous and Boraginaceous species, the aecial host range for this species can not be given with certainty. It is probable, however, that besides *Hydrophyllum capitatum,* which has been shown by culture to be an aecial host, other species of *Hydrophyllum* and species of *Phacelia* and *Nyctelea* will be found to belong here, possibly connected with different races. Whether the Boraginaceous aecia of this country also belong here can only be settled definitely by cultures. It seems probable, however, that a part of these aecia will be found to be connected with rusts identical with or very similar to *Puccinia bromina* and *Puccinia secalina,* and presumably will be found to have their connections with *Bromus* and *Agropyron* rusts. *Puccinia Koeleriae* offers but little information as to its host range, as its aecial connection is founded on only one culture to *Mahonia Aquifolium,* and it is likely that other Berberidaceous species will be found to serve as hosts. A thorough understanding of these species can be reached only through the gradual accumulation of field evidence of associations such as those obtained by Mr. Bethel and Dr. Coons and by cultures to determine both grass and aecial hosts of such rusts. The presence or absence of races and their limitations within the species and the limitations and relations of the species to each other can be determined only by such methods.

To Prof. H. S. Jackson the writer is indebted for helpful suggestions from his knowledge of western rusts. Dr. J. C. Arthur especially has given many helpful suggestions, drawn from his large acquaintanceship and work with this group. The writer also is indebted to Mr. E. Bethel and Dr. G. H. Coons for their discriminating field observations and for material.

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